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OPINION PAPER

Seasonal bulk xylem pressure in temperate broadleaf eudicot trees: a case study for sugar long-distance transport and signaling

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Abstract

Sugars regulate growth, development, and defense in trees. Sugars are also important signaling molecules and are transported over long distances via xylem and phloem. Sucrose loading to tracheids and vessels is associated with bulk xylem pressure and occurs seasonally in temperate broadleaf eudicot trees. Following restoration of xylem hydraulic conductivity in spring, sugars are unloaded from xylem sap at apical branches and deposited as starch before growth of shoot apical meristems. Growth of cambia and shoot apical meristems leads to starch catabolism that yields hexose-phosphates to fuel cell growth and regulate other signal networks. The contrast between cell molecular biology of *Arabidopsis* and physiology of temperate broadleaf eudicot trees indicates the importance of phosphorylation in long-distance sugar signaling. Hexokinase, acting as a hub for signal and hormone networks, is likely an important regulator of sugar signaling in response to stimuli such as energy status, sugar status, and environmental conditions. The comparative analysis suggested here could help bridge physiology and detailed molecular mechanisms regarding physiology of trees.

Keywords Sugar signaling · Hexokinase · Long-distance transport · Tree

Introduction

Long-distance signaling in plants is correlated with many cellular and whole plant functions including growth, reproduction, defense, and hormone response (Aki et al. 2008; Eveland and Jackson 2012; Mason et al. 2014). Sugars can be used as carbon skeletons for the biosynthesis of organic molecules and as transient energy storage (Chen et al. 2015). For example, *Arabidopsis* deposits 30–50% of photoassimilates as starch during the day to be remobilized the subsequent night for carbon and energy metabolism (Ramon et al. 2008; Stitt et al. 2012). Non-structural carbohydrates (NSCs), including mono-, di-, oligo-, and polysaccharides, are products of photosynthesis (Plavcova et al. 2016) and can behave as signal and transport molecules. Sugar transporters, SWEETs specifically, are conserved from archaebacteria to plants and animals (Chen et al. 2015). In angiosperms, NSCs are implicated in signal responses to diurnal, environmental, and seasonal stimuli (Chen et al. 2015; Li and Sheen 2016), with similar observations in the SAR clade (Schiener et al. 2015).

In temperate broadleaf eudicot trees, spring xylem sucrose loading is implicated with bulk xylem pressure that restores xylem hydraulic conductivity. At apical branches, sugars are unloaded from xylem sap and deposited as starch in ray and axial parenchyma (RAP). Catabolism of starch contributes to sugar signals upon growth of cambia or shoot apical meristems (Li and Sheen 2016; Rolland et al. 2006; Ramon et al. 2008). Sugar signaling appears to mediate cell energy status, sugar status, and response to environmental conditions. By comparing molecular evidence from *Arabidopsis* with physiology in temperate broadleaf eudicot trees following winter dormancy, we show the importance of kinase activity in long-distance sugar signaling. Phosphorylation mechanisms, especially via hexokinase (HXK), likely play an important role. We suggest that cluster-based modeling may help our understanding of long-distance sugar signaling in temperate broadleaf eudicot trees.

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Table 1 Temperature-dependent xylem loading and unloading of NSCs in temperate broadleaf eudicot trees with mode of seasonal bulk xylem pressure identified

Plant	Pressure	Xylem loading (°C)	Xylem unloading (°C)	Reference
Acer saccharum Marsh	Stem and root pressure	Loading of sucrose at 0 to 22 °C	Unloading of sucrose and hexoses at 22 to 40 °C	Sauter et al. 1973
Juglans regia L.	Stem and root pressure	Loading of sucrose at 0 to 15 °C	Unloading of sucrose at temperatures > 15 °C	Améglio et al. 2000, 2004; Ewers et al. 2001; Decourteix et al. 2006
Betula pendula Roth	Root pressure only	Loading of soluble NSCs at 0 to 20 °C	Unloading of glucose and fructose at temperatures > 20 °C	Sauter and Ambrosius 1986
Salix	Root pressure only	Loading of soluble NSCs at 2 to 21 °C	Unloading of hexoses and sucrose at temperatures > 21 °C	Sauter 1981, 1982
Populus × *canadensis* Moench cv. "robusta"	Bulk xylem pressure not reported (root pressure assumed)	Loading of soluble NSCs at − 2 to 10 °C	Unloading of hexoses including maltose at temperatures > 10 °C	Sauter 1988
Populus nigra L.	Bulk xylem pressure not reported (root pressure assumed)	Xylem loading of glucose at 0 to 10 °C	Unloading of hexoses at temperatures > 10 °C	Furukawa et al. 2011

Sucrose loading through facilitated diffusion to xylem

Vascular plants typically utilize phloem for bulk transport of soluble NSCs to carbon sinks. However, xylem sap in temperate broadleaf eudicot trees is also known to provide a route for NSCs following dormancy and prior to leaf out (Essiamah and Eschrich 1986; Aloni 1987). Rapid carbon transport can be accomplished via xylem sap and loading of soluble NSCs to vessels (Evert and Eichhorn 2006; Heizmann et al. 2001; Mason et al. 2014). In temperate broadleaf eudicot trees, late winter and early spring positive temperatures signal efflux or loading of sucrose to xylem sap via facilitated diffusion from high concentrations stored in RAP. High concentration of soluble sucrose is maintained in RAP at sub-zero winter temperatures for freeze avoidance or tolerance (Améglio et al. 2004; Plavcova and Jansen 2015; Sauter 1982).

RAP are derived from fusiform and ray cambial initials, are alive at maturity, and have been implicated in storage and regulation of NSCs between phloem and xylem (Morris et al. 2016; Plavcova and Jansen 2015; Plavcova et al. 2016). Xylem pit membranes are porous to sucrose and lignified secondary cell walls of xylem vessels provide an effective barrier for molecules of a similar or greater mass than sucrose (Cirelli et al. 2008). Thus, sucrose confined to xylem vessels lowers water and osmotic potential of vessels, generating bulk xylem pressure and sap movement to apical branches. Temperature-dependent xylem loading and unloading of NSCs is well documented in temperate broadleaf eudicot trees, notably in species with seasonal bulk xylem pressure (root and/or stem pressure). Some examples are included in Table 1.

Temperature-dependent loading and unloading of NSCs to vessels is implicated with spring carbon mobilization to cambia and shoot apical meristems following dormancy. Soluble NSC concentrations of vessel sap are typically highest in spring due to the strong carbon sinks (sugar demand) generated by shoot apical meristems (Heizmann et al. 2001). However, starch deposition at apical branches is positively correlated with xylem sap sugar content at shoot apices (Tixier et al. 2017), and catabolism is associated with growth of shoot apical meristems thus implicating coordination and regulation of sugar signals with other stimuli.

NSC unloading through active transport and starch deposition at apical branches

Sugar maple (*Acer saccharum* Marsh.) and European walnut (*Juglans regia* L.) unload NSCs from xylem sap and deposit starch in RAP of apical branches after sap flow from root or stem pressure and before growth of shoot apical meristems (Wong et al. 2003; Decourteix et al. 2008; Bonhomme et al. 2010). After restoration of xylem hydraulic conductivity via bulk xylem pressure, the sucrose transporter JrSUT1 (*Juglans regia* putative sucrose transporter 1) decreased sucrose concentration of vessel sap via unloading of sucrose to RAP (Decourteix et al. 2006). Low levels of soluble sugars in spring vessel sap of European walnut coincided with starch deposition in RAP (Decourteix et al. 2008) with minimum starch content observed after leaf expansion (Bonhomme et al. 2010). SUT is a family of sucrose transporters with different affinities (Aoki et al. 2003; Lalonde and Frommer 2012). However, in sugarcane (*Saccharum spontaenum* L.), SsSUT1 was also associated with unloading from vascular tissue and was highly selective for sucrose but with low affinity (Zhang et al. 2016). Walnut vessel-associated ray parenchyma cells of apical shoots demonstrated localization of JrSUT1 before growth of shoot apical meristems (Decourteix et al. 2008). Serving as conducting channels early in spring development, bud traces consist of two strands of procambial cells going to the shoot apical meristem (Evert and Eichhorn 2006). Reabsorption of NSCs transported in xylem sap via SUT is apoplastic and once in parenchyma transport can occur symplastically via plasmodesmata (Plavcova and Jansen 2015). The location of local NSC reserves for shoot apical meristem carbohydrate availability may therefore be in the bud itself or neighboring tissues of the stem (Bonhomme et al. 2010). Radial movement of NSCs when vascular cambial growth slows probably occurs with symplastic transport to shoot apical meristems (Améglio et al. 2002; Decourteix et al. 2008). Studies with walnut demonstrated high xylem sap sugar content just prior to growth of shoot apical meristems, with increased active sucrose uptake by xylem parenchyma cells at shoot apical meristems when compared to shoot axillary meristems. At the same time, xylem parenchyma cells of the apical portion of the shoots exhibited greater amounts of both transcripts and proteins of JrSUT1 than those of the basal stem segment. Conversely, no pronounced difference was found for putative hexose transporters JrHT1 and JrHT2 (*Juglans regia* hexose transporters 1 and 2). These findings demonstrate the high capacity of growing shoot apical meristems to import sucrose and seems to indicate that sucrose may play a much more significant role in carbon allocation as apical stems display little active glucose uptake (Decourteix et al. 2008). Here, xylem sugar transport and phloem backflow of water in the absence of transpiration (and when leafless) supports a "whole tree" approach to xylem and phloem as a single network (Tixier et al. 2017).

Extrapolation of *Arabidopsis* NSC signaling to physiology of temperate broadleaf eudicot trees

Cell-based assays and functional genomic screening have significantly facilitated the comprehensive understanding of the complexity of signaling processes (Baldazzi et al. 2012; Xing and Wang 2015). Meanwhile, the massive influx of information in model organism studies helps us understand a particular signaling process and network in other species. Sugar signaling in the loading and unloading process in *Arabidopsis* may represent a system for us to extrapolate from a signaling network to physiological changes in temperate broadleaf eudicot trees.

In *Arabidopsis*, sucrose import to cells can be symplastic (through plasmodesmata) or apoplastic (re-entering across the cell membrane and with H^+-ATPase as primary force) transport (Rolland et al. 2006). In *Arabidopsis* leaves, cytoplasmic sucrose and trehalose-6-phosphate (T6P; a signal of endogenous sucrose) can signal starch synthesis from hexose-phosphates via upregulation of the large subunit of ADP glucose pyrophosphorylase (AGP), promoting redox-dependent activation of AGP (Li and Sheen 2016; Ramon et al. 2008). Hexose-phosphates for starch deposition are produced following sucrose cleavage by cytoplasmic (neutral or alkaline) invertase to produce glucose and fructose, or hydrolysed by sucrose synthase (SUS) in the presence of UDP to produce fructose and UDP glucose (Rolland et al. 2006; Sturm and Tang 1999). SUS can be localized to the cytoplasm or, when dephosphorylated, is plasma membrane-associated (Sturm and Tang 1999). Even before intracellular import, sucrose can be cleaved by cell wall invertase to produce glucose and fructose (Rolland et al. 2006). Extracellular glucose and fructose enter the cell via hexose transporters that are co-expressed with cell wall invertase (Rolland et al. 2006; Sturm and Tang 1999). The primary glucose sensor, HXK, is implicated in signaling and metabolism of glucose to hexose-phosphates that will be used for starch synthesis (Li and Sheen 2016). Often associated with mitochondria, HXK1 is present in high molecular weight complexes including the nucleus where it regulates transcription, with a specific isoform also found in plastids (Ramon et al. 2008). Thus, we speculate that in temperate broadleaf eudicot trees, following unloading of sucrose to the cytosol of RAP via SUT at apical shoots, sucrose metabolism by SUS leads to accumulation of hexoses that can yield hexose-phosphates including UDP glucose (Fig. 1). Similarly, we speculate that hexoses cleaved from sucrose at the cell wall are transported to the cytosol, where their metabolism and that of UDP glucose yields hexose-phosphates to fuel starch synthesis or regulate other sugar signal networks. Glucose-6-phosphate (G6P) and UDP glucose can be synthesized to T6P, which upregulates AGP in the presence of cytosolic sucrose and in association with sucrose nonfermenting1-related kinase1 (SnRK1), an energy sensor, to induce starch deposition and sucrose-induced upregulation of SUS (Li and Sheen 2016; Ramon et al. 2008; Rolland et al. 2006; Stitt et al. 2012). SUS activity, which is positively correlated with starch content in potato tubers (Sturm and Tang 1999) and associated with sucrose/T6P/SnRK1 signaling (Li and Sheen 2016; Ramon et al. 2008; Rolland et al. 2006), likely governs sink strength via starch deposition.

When shoot apical meristems and vascular cambia have limited growth (e.g., in early spring, prior to favorable growing conditions), starch synthesis and phloem backflow at apical shoots maintains sugar and water flux between xylem and phloem and NSC delivery to shoot apical meristems (or vascular cambia) to fuel growth once favorable growing conditions start later in spring. When growth of shoot apical meristems produces photosynthetic leaves, the source status of tissues changes from starch/soluble NSCs stored in RAP of apical branches to photoassimilates produced by newly photosynthetic tissues. Thus, spring starch synthesis, observed in weeks of reduced meristematic and cambial growth, is a

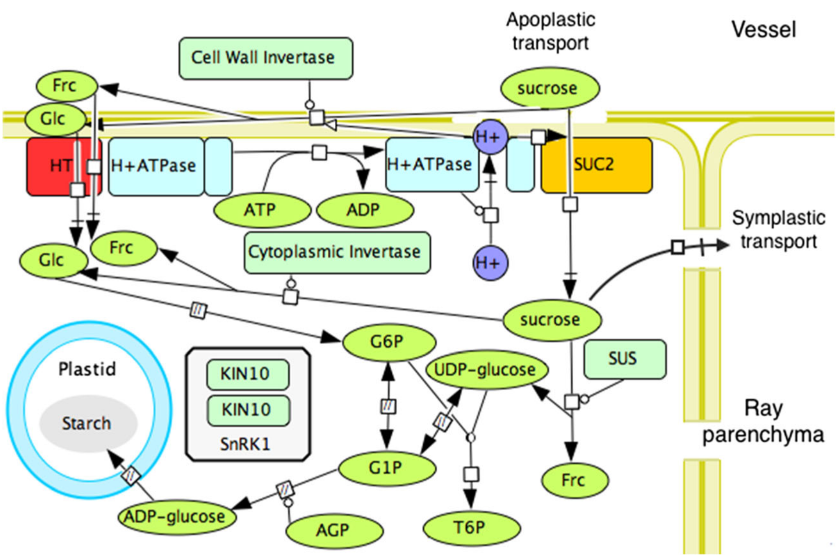

Fig. 1 Hypothetical model of sugar signal networks (derived from protein interactions identified in *Arabidopsis*) associated with starch synthesis in temperate broadleaf eudicot tree shoot apices prior to growth of shoot apical meristems and following seasonal bulk xylem pressure. Unloading of vessel-loaded sucrose to ray parenchyma at apical branches is apoplastic at pit pores via trans-membrane SUC2 (orange) sucrose symporters. Cytoplasmic sucrose (which can be transported symplastically via plasmodesmata) is cleaved by cytoplasmic invertase to glucose (Glc) and fructose (Frc) or hydrolyzed by sucrose synthase (SUS) to UDP glucose and fructose. Apoplastic sucrose is also cleaved by cell wall invertase to produce glucose and fructose that enters the cytoplasm via HT hexose symporters (red). In the cytoplasm, UDP glucose or glucose can be metabolized to hexose-phosphates to fuel starch synthesis or may be regulated based on signal networks with energy sensors such as KIN10/11 catalytic subunits of the plant sucrose nonfermenting1-related kinase (SnRK1). Symplastic transport occurs via plasmodesmata. Arrow with bar and open box = transport, open box and circle = catalysis, box containing hash marks = known transition omitted, open arrow = physical stimulation (i.e., pH)

transient sink to be mobilized as a source for growing shoot apical meristems. Likewise, autumn starch deposition occurs when meristems and cambia have limited growth due to the onset of dormancy. Rather than source activity, upregulation of sucrose-6-phosphate-synthase (SPS) leads to starch degradation and autumn production of soluble sucrose for freeze tolerance or avoidance. In spring, SPS mobilizes starch reserves to sinks (Plavcova and Jansen 2015),

Table 2 Protein-protein interactions predicted by STRING analysis based on comparison of molecular evidence from *Arabidopsis* to physiology observed in temperate broadleaf eudicot trees following dormancy

Protein	Function
ABI2 (ABA insensitive 2)	Repressor of the abscisic acid (ABA) signaling pathway
ADG1 (ADP glucose pyrophosphorylase 1)	Synthesis of starch
BZR1 (BRASSINAZOLE-RESISTANT 1)	Transcriptional repressor that binds to the brassinosteroid response element
CWINV2 (cell wall invertase 2)	Cleaves sucrose
GAI (GA insensitive)	Transcriptional regulator that acts as a repressor of the gibberellin (GA) signaling pathway
HXK1 (hexokinase 1)	Sugar sensor which may regulate sugar-dependent gene repression or activation
KIN10 (SNF1 kinase homolog 10)	Catalytic subunit of the probable trimeric SNF1-related protein kinase complex
KIN11 (SNF1 kinase homolog 11)	Catalytic subunit of the probable trimeric SNF1-related protein kinase
PIF4 (transcription factor PIF4)	Negative regulator of phytochrome B-mediated process
SPS3F (sucrose-phosphate-synthase)	Sucrose synthesis
SSA (sucrose synthase 2)	Sucrose synthesis
STP1 (sugar transporter 1)	Major hexose transporter
SUC2 (sucrose-proton symporter 2)	Sucrose transport
SUS1 (sucrose synthase 1)	Sucrose-cleaving enzyme
TPS1 (trehalose-6-phosphate-synthase)	Glucose sensing and signaling
TRE1 (trehalase 1)	Regulation of trehalose content by hydrolyzing trehalose to glucose
UGP1 (UDP glucose pyrophosphorylase 1)	Converts glucose 1-phosphate to UDP-glucose

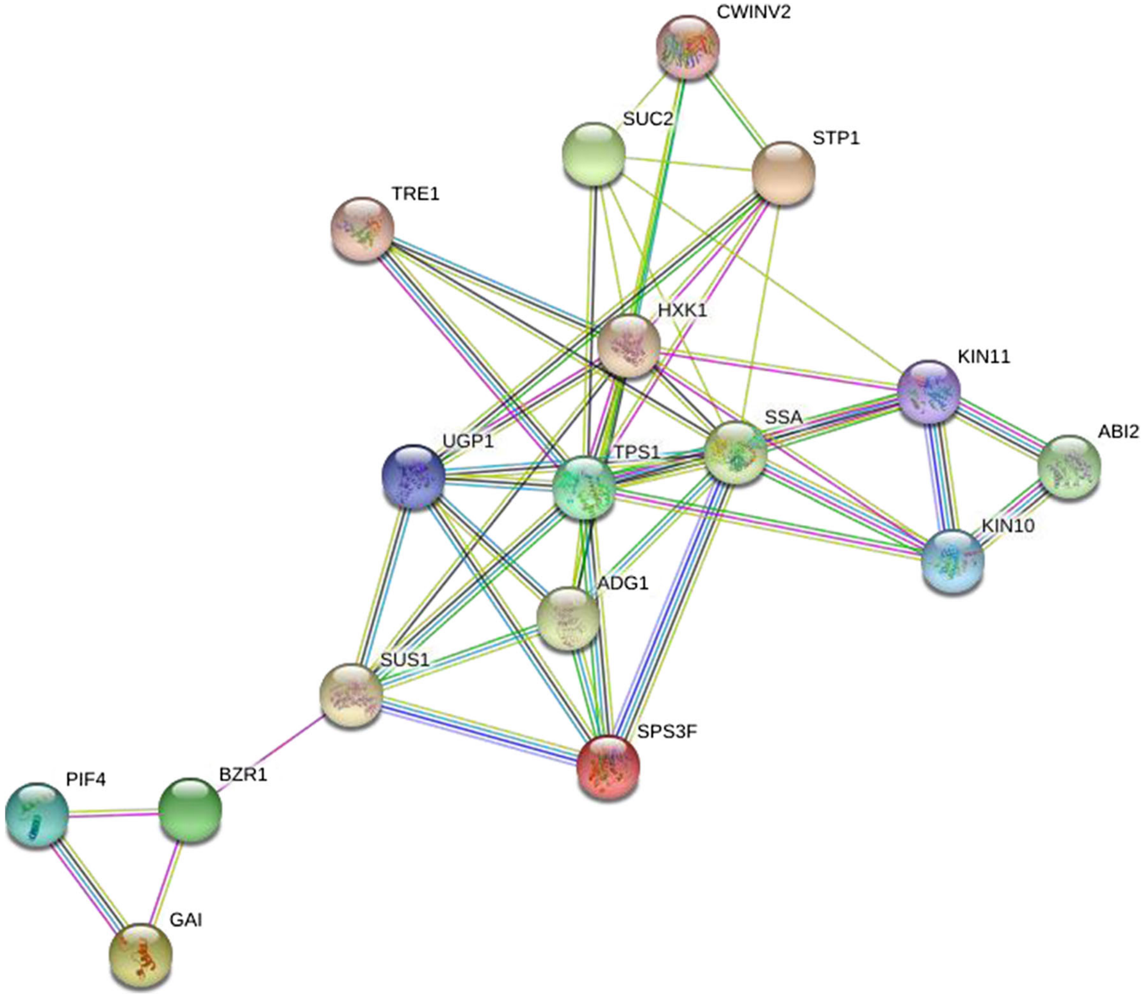

Fig. 2 Protein-protein interactions in apoplastic transport of sucrose via SUC2 and of hexoses via STP1. Sucrose cleavage at the cell wall (CWINV2) or in the cytoplasm (SUS1, SSA) yields hexose-phosphates, and HXK1 as a receptor regulates transduction based on energy status (KIN10, KIN11), sugar status (TPS1, TRE1), hormone status (BZR1, GAI, ABI2), and environmental conditions (PIF4). The response is regulation of metabolism, or synthesis of polysaccharides such as sucrose (SPS3F) or starch (UGP1, ADG1). Edge colors: pink = known experimentally determined protein-protein interaction (see Appendix A, List 1), light blue = known metabolic pathways, protein complexes, signal transduction pathways, etc. from curated databases (Appendix A, List 2), black = predicted protein-protein interaction from co-expression of homologs in other species (Appendix A, Fig. 1), yellow = text-mined PubMed abstracts and full-text excerpts for protein name mention associations (see Appendix A, List 3), and purple = homology between proteins

the strongest sink being developing shoot apical meristems and cambia (Bonhomme et al. 2010; Decourteix et al. 2008; Plavcova and Jansen 2015). Vascular cambia of ring-porous species may represent more important sinks than developing shoot apical meristems because significant cambial growth occurs prior to leaf out (Panchen et al. 2014; Plavcova and Jansen 2015). Ring-porous *Robinia pseudoacacia* L. has upregulated SUS at vascular cambia to produce UDP glucose from soluble sucrose for cell wall synthesis of new xylem conduits (Plavcova and Jansen 2015). SUS isoforms have developmental- and organ-specific expression, but are largely known for feeding sink metabolism (Sturm and Tang 1999) and probably are active in cell expansion at shoot apical meristems of diffuse-porous species too.

Sugar signal transduction

The Search Tool for the Retrieval of Interacting Genes/Proteins (STRING) database allows for investigation of protein-protein interactions (PPI) (Szklarczyk et al. 2017) and was applied to PPI analysis in our previous work (Conroy et al. 2013). Seasonal bulk xylem pressure and long-distance transport of sugars in temperate broadleaf eudicot trees provide a system to understand sugar signal networks and their coordination with hormonal and environmental stimuli. Thus, a literature review of sugar regulatory networks in *Arabidopsis* was contrasted to physiology observed in temperate broadleaf eudicot trees following dormancy, identifying 17 proteins of interest (Table 2). (See Fig. 2 for the protein association network of all 17 proteins applied to

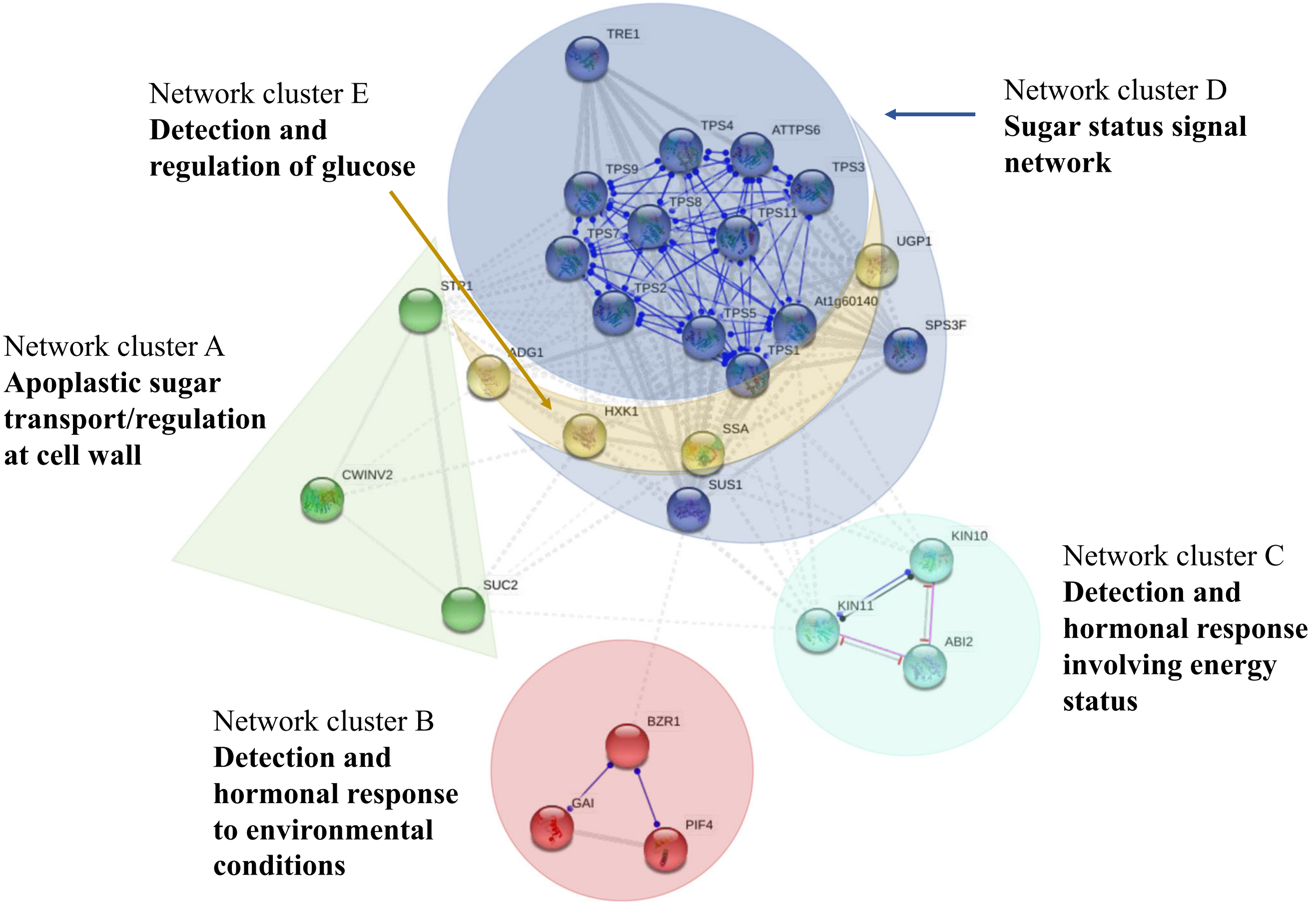

Fig. 3 Functional clusters from STRING analysis. Green (network cluster A) = apoplastic sugar transport/regulation at cell wall; red (network cluster B) = hormonal response to environmental conditions; teal (network cluster C) = hormonal response involving energy status; blue (network cluster D) = sugar status signal network; yellow (network cluster E) = glucose and regulation for polysaccharide synthesis. Edge colors: blue = bonding, pink = post-translational modification, red = inhibition. Solid dots signify that the mode of action is unspecified and a bar indicates negative regulation (see Appendix A, List 1 for known experimentally determined protein-protein interaction action type and effect of first shell of protein-protein interactions; note KIN10, KIN11, ABI2 protein-protein interactions omitted as the interaction is either insignificant or no experimental data is found in *Arabidopsis thaliana*, but putative homologs were found interacting in other species). Gray = text-mined PubMed abstracts and full-text excerpts for protein name mention associations; thickness/dashes designate ranking of mentions (see Appendix A, List 3)

STRING analysis.) We first applied *Arabidopsis thaliana* (At)-sucrose-proton symporter 2 (SUC2) to STRING because SUT has been characterized in temperate broadleaf eudicot trees along with localization and upregulation in apical branches following dormancy (Decourteix et al. 2006, 2008; Rolland et al. 2006; Williams et al. 2000). At warmer spring temperatures, sucrose is cleaved to hexoses in temperate broadleaf eudicot tree sap (Furukawa et al. 2011; Sauter 1982, 1983, 1988). Thus, At-cell wall invertase 2 (CWINV2) and At-sucrose synthase 1 and 2 (SUS1 and SSA) were added to STRING analysis along with At-hexose transporters (STP1) and At-sugar sensors (HXK1). Further insight was gained through inclusion of At-trehalose signaling (TPS1 and TRE1; cell sugar status) and At-KIN (KIN10 and KIN11; energy status) proteins (Li and Sheen 2016). As described previously, studies with temperate broadleaf eudicot trees also indicated that starch was synthesized after sugars were translocated in xylem sap and before growth of shoot apical meristems (Decourteix et al. 2008; Bonhomme et al. 2010; Wong et al. 2003). Thus, we investigated At-starch (UGP1, ADG1) and At-sucrose regulatory pathways (SPS3F) that may provide insight to seasonal cues involved in the regulation of NSCs in temperate broadleaf eudicot trees such as daylight and (more specifically) temperature (Sauter 1981, 1982, 1983, 1988; Améglio et al. 2000, 2004; Ewers et al. 2001). Evidence in *Arabidopsis* further implicated brassinosteroid interactions (BZr1) associated with dark- and heat-activated transcription factors (PIF4) (Oh et al. 2012; Pien et al. 2002). At-GAI was also included in STRING analysis, implicated by the existence of gibberellic acid (GA) in spring temperate broadleaf eudicot tree sap (Sheldrake and Northcote 1968; Furukawa et al. 2011). Finally, At-ABI2 was tested by STRING as the association of abscisic acid (ABA) with growth of shoot apical meristems (Rinne et al.

1994; Furukawa et al. 2011), water status, and drought resistance (Schill et al. 1996; Umezawa et al. 2010) has recently been implicated with plant sugar status (Li and Sheen 2016).

We hypothesize that when sucrose is unloaded from xylem sap of temperate broadleaf eudicot trees, signal perception likely relies on HXK acting as a receptor of glucose in the cell. We speculate that, at the cell wall, sucrose is subject to cleavage by cell wall invertase or by SSA following apoplastic transport to the cytoplasm. Hexose transporters typically are upregulated with cell wall invertase for apoplastic transport of hexoses following cleavage of sucrose. Thus, HXK may act as a receptor of glucose in the cytoplasm to transduce the signal based on various protein interactions that communicate cell energy status, sugar status, and environmental conditions such as heat and light. Signal response following transduction regulates cell metabolism, starch content, and sugar status. Termination of the signal is likely a reset of favorable conditions that signal completion of transduction and inactivation of HXK.

A network approach takes simplified cellular logic, includes directed or indirect potential interactions, and is based on improved statistical power on large-scale data. The protein association network produced in STRING analysis was thus enlarged and network edges were specified to molecular action (Fig. 3) that isolated interactions through functional clustering of proteins with *K*-means set to five. The generated interaction network for *Arabidopsis* gene subsets clearly shows three interaction network clusters connected to each other, and that they are involved in apoplastic transport of sugars (network cluster A), the detection of environmental conditions and hormonal responses (network cluster B), and the detection of energy status and of sugar for polysaccharide synthesis and/or signaling (network cluster C, D, and E). Phosphorylation mechanisms, especially via HXK acting as a hub, likely play an important role in sugar signaling networks. Transcriptional control of HXK function, however, seems to be associated with brassinosteroid presence, implicating downstream regulation of HXK by brassinosteroid or BZR1 (Kühn 2016). Hexokinase regulation via brassinosteroid interaction with the dark- and heat-activated transcriptional regulator PIF4 (Kühn 2016; Oh et al. 2012) seems consistent with NSC temperature-dependent (and thus seasonal) xylem loading and unloading observed in temperate broadleaf eudicot trees that implies heat and/or photoperiod detection. Additional to association with the transcriptional regulator PIF4, evidence exists that brassinosteroids are transcriptionally regulated by sugars (Kühn 2016; Oh et al. 2012). Furthermore, sucrose and glucose concentration, along with sucrose to glucose ratios, can potentially mediate important plant hormone responses. Recent evidence from peas (*Pisum sativum* L.) suggests that sugars and sink activity mediate the effect of auxin on apical dominance (Mason et al. 2014; Cookson et al. 2016). In tomato (*Solanum lycopersicum* L.) leaves, activity of cell wall invertase has been associated with cytokinin-mediated delay in leaf senescence and is also hypothesized to stimulate ABA-induced leaf senescence if hexose to sucrose ratio is low (Li et al. 2017; Ruan et al. 2010). Sugars evidently are important signals during long-distance transport, and they regulate plant development.

Concluding remarks

Seasonal bulk xylem pressure in temperate broadleaf eudicot trees provides a case study for long-distance transport and sugar signaling in plants. Physiology of seasonal bulk xylem pressure in trees is well documented, with molecular mechanisms of sugar signaling better elucidated in *Arabidopsis*. Contrasting molecular evidence and genomic data in a model system to observed physiology in other organisms may improve understanding of sugar signaling complexes. Furthermore, examining “case studies” in other organisms may provide innovative approaches for investigating regulators and molecular links of sugar signaling complexes in *Arabidopsis*. Phosphorylation appears to play an important role in mediating sugar signaling between other protein networks with hexokinase as a key regulator, yet evidence for activation or inhibition of hexokinase is still needed. Additionally, brassinosteroid interaction with hexokinase and with dark- or heat-activated transcription factors implicates hexokinase as a hub to coordinate response to stimuli, such as energy status, sugar status, and environmental conditions. NSC temperature-dependent (and thus seasonal) xylem loading and unloading observed in temperate broadleaf eudicot trees may provide indirect evidence of hexokinase as a central regulator of sugar signaling complexes. It is possible that such a comparative analysis could help bridge physiology and detailed molecular mechanisms and foresee the implementation of comparative analyses in the study of physiology of broadleaf eudicot trees and other land plants.

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